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Biology and Larvae of the Cleptoparasitic Bee *Townsendiella pulchra* and Nesting Biology of Its Host *Hesperapis larreae* (Hymenoptera: Apoidea)

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ABSTRACT

Townsendiella (*Townsendiella*) *pulchra* Crawford (Anthophoridae: Nomadinae) is a cleptoparasite of *Hesperapis* (*Panurgomia*) *larreae* Cockerell (Melittidae: Dasypodinae), the first confirmed host association of a *Townsendiella* species. *Hesperapis larreae* is a ground-nesting, solitary bee. Details of its nest structure, provisioning, and development are presented and compared with known information regarding other Dasypodinae. The first instar of the cleptoparasite, with most of the typical features of first-stage larvae of the Nomadinae, was recovered from the host nest, and its chorion was extracted from the host cell wall. A late-stage larva shares features with last instars of other nomadine taxa, especially *Neopasites* and *Neolarra*. Two dissected females of *T. pulchra* revealed 7 ovarioles per ovary, with totals of 5 and 4 mature oocytes per individual.

INTRODUCTION

On a brief field trip to Arizona, we encountered adults of *Townsendiella* (*Townsendiella*) *pulchra* Crawford (Anthophoridae: Nomadinae) in abundance as they searched the ground for host nests. Investigating the area further, we identified the host as *Hesperapis* (*Panurgomia*) *larreae* Cockerell (Melittidae: Dasypodinae). This paper (1) describes and discusses the nesting biology of the host in relation to other dasypodines, (2) presents information on the mode of parasitism of *T. pulchra,* and (3) describes the

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first- and late-stage larvae of the cleptoparasite. Little has been recorded about the behavior, ecology, and ontogeny of the two genera to which these species belong.

Michener (1936) found *Townsendiella (Eremopasites) californica* Michener "flying close over the ground in a colony of" *Hesperapis (Hesperapis) rufipes* (Ashmead), and R. R. Snelling (personal commun.) believes that *Conanthalictus* may be the host of the third known species of the genus, *Townsendiella (Xeropasites) rufiventris* Linsley. The association of *T. pulchra* with *H. larreae* is the first host association of *Townsendiella* confirmed by the recovery of immature cleptoparasites from host nests.

Immatures and nest components associated with this study are in the American Museum of Natural History, and adults (both in fluid and dried) are there and in the Smithsonian Institution.

ACKNOWLEDGMENTS

We express our appreciation to Barbara L. Rozen for her assistance in searching for nests of *Hesperapis larreae.* We thank G. I. Stage and R. R. Snelling for permitting us to read the biological section of their revision of *Hesperapis.* Information therein added substantially to our understanding of the behavior and ecology of a number of species in the genus. Snelling, Los Angeles County Museum of Natural History, also confirmed the identification of this *Hesperapis.* Richard H. Kruzansky provided the analyses of the nesting soils.

The manuscript has been critically reviewed by Roy R. Snelling and Byron Alexander.

DESCRIPTION OF SITES

We first discovered *Townsendiella pulchra* flying in association with *Hesperapis larreae* at 11 mi southwest of Congress, Yavapai Co., Arizona, on April 29, 1990. The single nest of *H. larreae* discovered there (fig. 1) was excavated on the following day. A second site (fig. 2), approximately 8 mi away, was identified May 3, 1990, at a place in Yavapai Co. 8 mi northwest of Wickenburg, Maricopa Co. Six nest entrances of *Hesperapis* were identified at this locality within a week, and four were traced to cells.

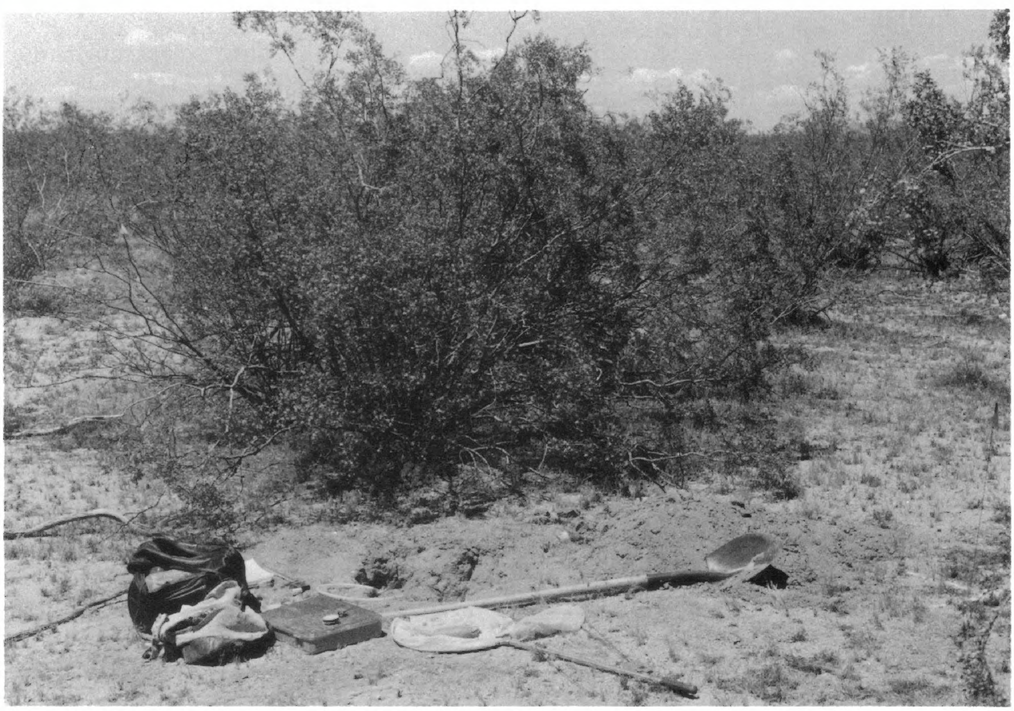
Although both sites contained a large number of plant species characteristic of the xeric Southwest (*Prosopis, Cercidium, Sphaeralcea*), creosote bush, *Larrea tridentata,* dominated the region. It was the pollen source for *Hesperapis larreae,* as well as for *Centris, Trachusa (Heteranthidium), Ancylandrena larreae* (Timberlake), and *Colletes.* Among cleptoparasites, several species of *Epeolus* and one each of *Triepeolus* and *Sphecodes* were collected while they flew in search of host nests. Several specimens of the rare *Hexepeolus rhodogyne* Linsley and Michener were netted at both sites. Of all cleptoparasites, *Townsendiella* was the most common when nests were found.

The *Larrea* plants were in maximum bloom at both sites at first discovery. At last visit on May 11, 1990, the *Larrea* at 11 mi southwest of Congress was almost totally past bloom and at 8 mi northwest of Wickenburg it was declining rapidly. We were unable to discover *Townsendiella* adults at either site at that late time.

Both sites occupied gently sloping ground in the predominantly creosote bush desert. All *Hesperapis* nests were on surfaces that sloped less than 10°. Although creosote bushes were widely distributed at both sites, searching *Townsendiella* tended to be concentrated, i.e., the cuckoo bees and presumably host nests were not found throughout the entire area occupied by creosote bushes. At the Congress site most *Townsendiella* were encountered within a radius of 30 m, and at the Wickenburg site, within a radius of approximately 50 m. At the Wickenburg site, nests of *Hesperapis larreae,* though few in number, were widely distributed within the 50 m radius.

The soil at both sites was a sandy loam derived from degraded igneous rock. At the Congress site it consisted of 62% sand, 29% silt, and 9% clay (coarse fragments >2 mm = 10.8%); at the Wickenburg site, 70% sand, 21% silt, and 9% clay (coarse fragments >2 mm = 8.0%).

The soil appeared dry at the surface and at cell level. The surfaces generally consisted of loose material, and the subsurface was irregularly consolidated. Large rocks were absent,



Figs. 1, 2. Nesting sites of *Hesperapis larreae*. **Top.** 11 mi southwest of Congress, Yavapai Co., Arizona. **Bottom.** 8 mi northwest of Wickenburg, Maricopa Co., Arizona.

and plant roots were uncommon. Nests were on nearly barren surfaces between creosote bushes except one which was at the base of a bush.

BIOLOGY OF *HESPERAPIS LARREAE*

The nest entrances of *Hesperapis larreae,* although usually hidden in small clumps of low (less than 8 cm high), dry herbaceous plants, were not extensively shaded by other vegetation including creosote bushes.

Finding nest entrances was difficult because they tended to be hidden under low-growing, dried plants and they did not possess obvious tumuli. We identified only two of the seven nest entrances by observing returning *Hesperapis* females entering them. We discovered all other nests because we observed one or more *Townsendiella* females perched near a potential nest entrance or returning repeatedly to one spot. *Townsendiella* females, when searching for nests, customarily investigated these low clumps of dried vegetation, which suggested that most nests were secreted this way. We saw one returning *Hesperapis* female enter its nest swiftly, without slowing and weaving. This observation and our inability to discover more than two females entering or leaving nests during a week of study by two persons suggest that comings and goings may always be rapid, perhaps a behavioral adaptation that lessens the chance of nest identification by predators and parasites.

Hesperapis and *Townsendiella* were active during the middle part of the day (9:00 a.m. to 4:00 p.m.), and from collection records their seasonal activity seems restricted mostly to the spring blooming of *Larrea.* However, Hurd and Linsley (1975) reported a female of *Hesperapis larreae* collected on *Larrea* on September 9 in Otero Co., New Mexico, and a female in the American Museum of Natural History was captured on *Larrea* on August 17 in Cochise Co., Arizona.

No nest was occupied by more than one female, and males were not found in nests.

NEST ARCHITECTURE: Main burrows were irregular in diameter, probably because of the uneven consolidation of the substrate, and ranged in diameter from 3.0 to 4.0 mm (N = 6). Entering the ground obliquely, they descended in a meandering and irregular path (figs. 4–6). The descent of one seemed vertical, but with all others the path was at about a 45° angle. Burrow walls were unlined and irregular.

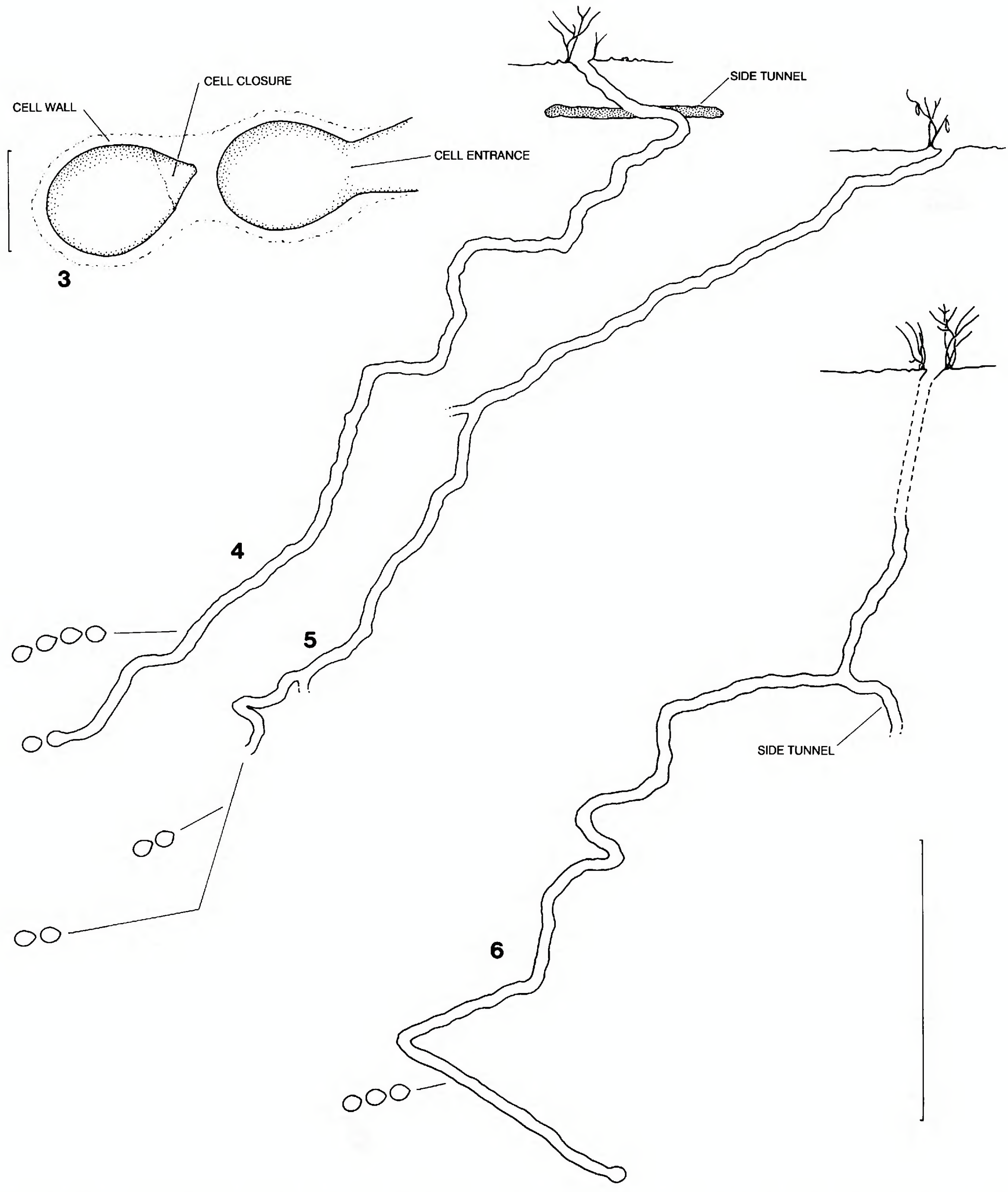
Main burrows were open, at least for the most part, and often revealed side branches (some soil-filled), particularly near the surface. We are uncertain whether some of these side tunnels may have been created by other insects, but other side tunnels almost certainly were the work of *Hesperapis,* perhaps aborted attempts of females to find their way through consolidated soil.

Although all traced side tunnels ended blindly (i.e., did not connect to cells), undetected filled side tunnels, probably branching deep in the ground, led to cells. Six nests contained two sets of cells in linear series, and one nest contained three such sets. In all five nests, the older cells were closer to the surface than the newer ones. Within a single series the newest cell was closest to the tunnel leading from it; the oldest cell was at the rear of the series.

Of the 11 separate series encountered in five nests, 1 consisted of four cells, 2 of three cells, 6 of two cells, and 2 of one cell (one of these was a complete series; the other represented the end cell of a series to which other cells presumably would have been added). The depths (cm) of the series in each of five nests were: 21, 23, 24; 22, 26; 24, 28; 26, 29; and 27, 32. Hence, in these five nests the within-nest differences between the depth of cell series ranged from only 1 to 5 cm.

Cells in series (fig. 3) were virtually end to end, there being no filled or unfilled burrow separating them. In one typical case the center of the cell closure was 1.0 mm from the rear of the cell in front of it. Nearly horizontal cells tilted toward the rear 10 to 20°.

Cells were symmetrical around their long axis, that is, the cell ceiling was not vaulted more than the floor. Their maximum diameter ranged from 5.0 to 5.3 mm (N = 5), and the length from rear to center of closure was 6.5 to 7.1 mm (N = 3). Their large diameter in relation to their length made them appear unusually globular compared with cells of many other bees. The diameter of a still open cell entrance was only 2.7 mm, which accentuated the robust appearance of this cell.



Figs. 3–6. Nest elements of *Hesperapis larreae*. **3.** Cell series consisting of a closed cell and an open one, side view. **4-6.** Examples of nests, side view. Scale lines refer to figures 3 (= 5 mm) and 4–6 (= 10 cm), respectively.

Walls (approximately 0.5 to 1.0 mm thick) of recently constructed cells, though fragile, tended to be slightly more consolidated than the substrate. Small sections of walls could often be carefully teased from the substrate for microscopic viewing. However, they could not be preserved unless extracted with substrate attached and then impregnated with a

mixture of white (casein) glue and water. Fresh walls were not waterproof and immediately absorbed water droplets. They were smooth, dull on the surface, and gave no hint as to what substance (if any) accounted for their slightly greater strength than the substrate. The soil of the cell wall was uniformly fine-grained in sharp contrast to the irregular particle size of the surrounding substrate. *Hesperapis* females are apparently capable of sorting out fine particles to construct the thin walls.

The cell walls from which mature (or nearly mature) larvae were removed were markedly different from the walls (and closure) of newly constructed cells. The altered cell walls are described below under Provisioning and Development.

Cell closures exhibited a number of unusual features. Like the inner surface of cell walls, they consist of uniformly fine material. They were deeply concave on the inside, and the concavity was cone-shaped (fig. 3). The surface of the cone was nearly continuous with the cell wall, and the two surfaces shared the same texture. The center point of the cone was almost pitlike when viewed from inside the cell. In contrast to the cell closures of most ground-nesting bees, the inner surface of the closure was nearly smooth, i.e., there was no distinct spiral contouring of this surface. However, by observing these closures in oblique light through a microscope, a vague spiral structure could be detected in some cases. Closures of newly constructed cells were fragile, consisting of poorly consolidated material throughout, but, as with cell walls, closures of cells containing older larvae were impregnated with some substance as is described below. Closures of three cells ranged from 3.2 to 3.5 mm in maximum diameter on the inside. The depth of the concave inner surface of four cells ranged from 1.5 to 1.8 mm.

PROVISIONING AND DEVELOPMENT: Females transported *Larrea* pollen and nectar as large moist masses on their hind legs. Early loads were apparently shaped and deposited as small spheres in the cells, as was also reported for *Hesperapis trochanterata* (Rozen, 1974; but see data regarding early provision load of *Dasypoda plumipes* in Lind, 1968). One preliminary provision sphere in an open cell measured 2.3 mm in diameter. Fully formed provisions were approximately spherical, uncoated, uniformly moist, and measured 3.1 to 3.5 mm in diameter (N = 10). These spheres rested on the cell floors.

The curved eggs of *Hesperapis larreae* were placed on the top of the provisions in the median longitudinal cell plane; their more rounded anterior ends faced the cell closures and the tapering posterior ends pointed toward the rear of the cell. The chorion was smooth, shiny, and transparent over the grayish-white egg. One egg measured 1.75 mm long and 0.45 mm in maximum diameter. Young larvae apparently crawl over the surface of the food sphere as they feed, for they possessed paired ventrolateral tubercles on the thoracic and most abdominal segments. Although older larvae cradled depleted food masses with their somewhat elongate bodies, other observations on larval behavior are required to understand feeding activities throughout the larval stage. Several larvae defecated soon after feeding and one survived to become a white, quiescent postdefecating form within a week after capture, indicating that the species probably overwinters in this state.

Either after feeding or perhaps shortly before finishing, large larvae produced a substance (source unknown but perhaps anal or salivary) that impregnated the cell wall and closure so that these structures became strong, took on a dark "wet" appearance, glistened in places, and became water-retardant. This substance possessed no pollen grains (at least at first) and a section of impregnated cell wall did not "dissolve" when submerged in water for several hours. Because of their new strength, cell walls and closures in this condition were extricated intact from the substrate.

One larva had started to apply fecal pellets over the inner surface of the cell wall before we collected it. Larvae did not produce cocoons (unless the glistening substance described above represents a modified salivary secretion). Certainly no silk threads were in evidence in cells, and the recessed labiomaxillary region of larval *Hesperapis* characterizes noncocoon-spinning larvae.

BIOLOGY OF *TOWNSENDIELLA PULCHRA*

Although the two *Hesperapis larreae* nesting sites were separated by only 8 mi, the *Townsendiella pulchra* population at 11 mi southwest of Congress was further advanced than the one at 8 mi northwest of Wickenburg. At the Congress locality no males of *Townsendiella* were encountered, and the outer edge of the anterior wings of collected females were nearly totally worn away. At the Wickenburg site males were not uncommon, and nearly half of the females still retained most of the outer wing margins.

At both localities females flew moderately slow, meandering paths close to the ground and halted or slowed near clumps of dried herbs as they sought *Hesperapis* nests. At the Wickenburg site, the flight of males could be identified because it was faster and less meandering though close to the ground. We observed no matings.

As stated above, we were able to observe *Townsendiella* females hovering around one point on the ground or perching near it. Often a female would wait several centimeters from an entrance, and then once in a while fly to the entrance, inspect it briefly, and then return to her perch. Two or three females behaved this way simultaneously at one spot without interacting with (e.g., chasing) one another. When we had the opportunity later, we were able to identify *Hesperapis* nest entrances at such places. In one case we captured both a female *Townsendiella* and a *Hesperapis* female as they emerged from a single nest.

Although *Townsendiella* was moderately abundant, particularly at the Wickenburg site, we recovered *Townsendiella* immatures from only four cells. However, a good many of the other cells were damaged in excavation so that immatures of neither host nor parasite were discovered, and a few cells were open or freshly closed.

One of the *Townsendiella* larvae was a first instar with the following characteristics: head capsule elongate, sclerotized, moderately pigmented, semiprognathous; vertex projecting immediately in front of sharply constricted posterior margin (also characteristic of *Neopasites*; see description of late-stage larva); long paired labral tubercles present; antennae nonprotuberant; mandibles elongate, curved, sharply pointed; maxillary palpi conspicuous; labial palpi indistinguishable; most abdominal segments (but not thoracic segments) with paired ventrolateral tubercles, and terminal abdominal segment not distinctly forked but with single median elongate projection and with two less elongate lateral projections. A detailed description of this specimen will be prepared later in conjunction with a proposed comparative examination of the first instars of the Nomadinae by JGR.

The two other *Townsendiella* larvae were probably second instars and in one cell the cast skin and head capsule of the first instar were recovered. In the second instar, the head capsule was no longer pigmented, mandibles were short, and the projecting venter of abdominal segment IX had developed. The labral tubercles, though shorter, were still in evidence as were the ventrolateral abdominal tubercles.

A single large *Townsendiella* larva was recovered from the fourth cell which still contained a large provision mass. The larva was superficially so similar to host larvae of similar size that JGR misidentified it at first. Only after he saw its short mandibles and distinct, if small, labral tubercles did he correctly recognize it. The specimen is a penultimate instar or a young last instar. Whichever instar it may be, its features suggest relationships between the Townsendiellini and some other nomadine tribes. For this reason it is described, illustrated (figs. 7–12), and compared with last-stage larvae of certain other Nomadinae at the end of this paper.

Also in one of the parasitized cells, the egg insertion hole (0.175 mm in diameter) of a *Townsendiella* was discovered in the cell wall. When the section of the wall containing this hole was submerged in water, the cast chorion was retrieved. The transparent colorless chorion with the hole at one end was 1.0 mm long.

Two freshly killed females of *Townsendiella* were dissected so that their ovaries could be examined. Each had seven ovarioles

per ovary (i.e., 7:7). One had a total of 5 mature oocytes,[3] the other 4 mature oocytes. Egg index (based on the definition of mature oocyte in footnote 3) (i.e., egg length of largest mature oocyte divided by the mean mesosomal width, Alexander and Rozen, 1987) was 0.69. Oocytes (fig. 13) measured 1.05–1.18 mm (N = 2) and were slender, rounded anteriorly, and somewhat tapering posteriorly. They exhibited no operculum or other unusual structures except that each bore a small raised area, nipplelike and not hook-shaped, at the anterior end. The chorion was smooth, nonreticulate, and shiny.

DISCUSSION OF BIOLOGY

Nesting biologies of the following species of Dasypodinae have been studied:

Dasypodini:	
Dasypoda plumipes Panzer	Müller (1884)
	Malyshev (1927)
	Lind (1968)
Hesperapis (*H.*) *rufipes* (Ashmead)	Stage and Snelling (MS)
H. (*H.*) *trochanterata* Snelling	Rozen (1987)
H. (*H.*) unnamed species	Stage and Snelling (MS)
H. (*Amblyapis*) *ilicifoliae* (Cockerell)	Stage and Snelling (MS)
H. (*Panurgomia*) *larreae* Cockerell	present paper
H. (*P.*) *nitidula* Cockerell	Stage and Snelling (MS)
H. (*P.*) *pellucida* Cockerell	Stage and Snelling (MS)
H. (*P.*) *regularis* (Cresson)	Burdick and Torchio (1959)
	MacSwain et al. (1973)
	Stage and Snelling (MS)
H. (*P.*) unnamed species	Stage and Snelling (MS)
Capicola braunsiana Friese	Rozen (1974)
Sambini:	
Haplomelitta ogilviei (Cockerell)	Rozen (1974)

Although available nesting information is too scanty to provide an overview of the nesting biology of the Dasypodinae, certain behavioral features of *Hesperapis larreae* are noteworthy. Linear cell arrangement has not been reported for any other *Hesperapis*, all of which construct single cells at the ends of branches. Cell series, however, were noted for *Capicola braunsiana*. The large cell diameter relative to length is not characteristic of most bees but has also been reported for *H. pellucida* and perhaps other species in the genus.

Walls of fresh cells of *Hesperapis larreae* are smooth, dull, and composed of soil much finer and more evenly grained than the substrate. They contrast sharply with the rough unlined cells walls of *H. trochanterata*. Stage and Snelling (MS) noted that the walls of *H. pellucida* "did not seem to be particularly smoothed or compacted." They reported that those of *H. ilicifoliae* seemed to be "lined with fine soil," perhaps smoothed with the tongue and "impregnated with saliva which made it harder and darker than the adjacent matrix . . . it readily absorbed drops of water though not as quickly as did the adjacent matrix." At one site, "the cell walls were so strong that it was possible to remove some of them intact." Stage and Snelling stated that the cell walls of *H. rufipes* were like those of *H. ilicifoliae* and were apparently smoothed in the same way. Hence in the genus some species (*trochanterata* and *pellucida*) have rough cell walls not coated with fine soil, whereas others (*larreae, ilicifoliae,* and *rufipes*) have smooth, fine-textured walls. The hardness and water-absorbing qualities of the smooth walls will have to be restudied in light of the fact that we now know water absorption, strength, and even color in a cell of *H. larreae* are modified by actions of the mature or nearly mature larva. Consequently, wall characteristics reported for other species of *Hesperapis* as well as for *Capicola braunsiana* and *Haplomelitta ogilviei* may not have been the result of the adult activity. Cell walls of *Dasypoda plu-*

[3] Mature oocytes as here defined were those that had taken on their final size and shape and had developed a visible, slightly shiny chorion. They were quite distinctive and presumably are Iwata's (1955) Category A oocytes. Slightly larger and also smaller oocytes without nutritive cells but also without chorions were also present in *Townsendiella.* These oocytes were a less well-defined group and probably conform to Iwata's Category B. Alexander and Rozen (1987), in their study of oocytes of parasitic bees, grouped Categories A and B together because they were difficult to distinguish. This was not a problem with *Townsendiella,* perhaps because specimens were fresh.

mipes are like the newly constructed walls of *H. larreae,* i.e., dull, smooth, and absorptive.

Cell closures of *Hesperapis larreae* were deeply concave on the inside and were essentially smooth, i.e., without a distinct spiral structure. Similar closures have been reported for *Capicola braunsiana* and *Haplomelitta ogilviei.* Closures of *Dasypoda plumpies,* while deeply concave, exhibit a distinct spiral.

The behavior of *Townsendiella pulchra* conforms with that of other Nomadinae. Females search for host nests and almost certainly enter them when host females are away—as indicated by *Townsendiella* females waiting or repeatedly returning to nest entrances. We are uncertain whether waiting cleptoparasites are an indication that the host female is in the nest. Possibly a cleptoparasite cannot detect the presence of a host female in the nest unless she sees the host depart.

The single chorion embedded in the cell wall confirms that, like other Nomadinae, *Townsendiella* inserts its egg there, presumably while the host female is away foraging. The *Townsendiella* first instar is hospicidal, as are those of all known Nomadinae. It possesses the major characteristics of the others with the interesting exceptions of a differently modified abdominal apex and the presence of paired ventrolateral abdominal tubercles—both features presumably associated with locomotion. Neither of these features have been reported for other Nomadinae, but first instars of the subfamily are poorly known. Specifically, first instars of *Neopasites* and *Neolarra* have yet to be examined. Considering the similarities in the following description between the late-stage larva of *Townsendiella pulchra* and last instars of representatives of *Neopasites* and *Neolarra,* first instars of the latter two taxa might clarify the phylogenetic relationships of the Townsendiellini, Biastini, and Neolarrini. Interestingly, early instars of the host also possess paired ventral tubercles on the abdominal segments as well as on the three thoracic segments.

LATE-STAGE LARVA OF *TOWNSENDIELLA PULCHRA*

Figures 7–12

Although we are uncertain as to whether the specimen described here is a last instar, it bears such a strong resemblance to the last-stage larvae of *Neopasites cressoni* Crawford and *Neolarra pruinosa* Ashmead (Rozen, 1966) that comparisons with these taxa may be valid and potentially revealing of relationships.

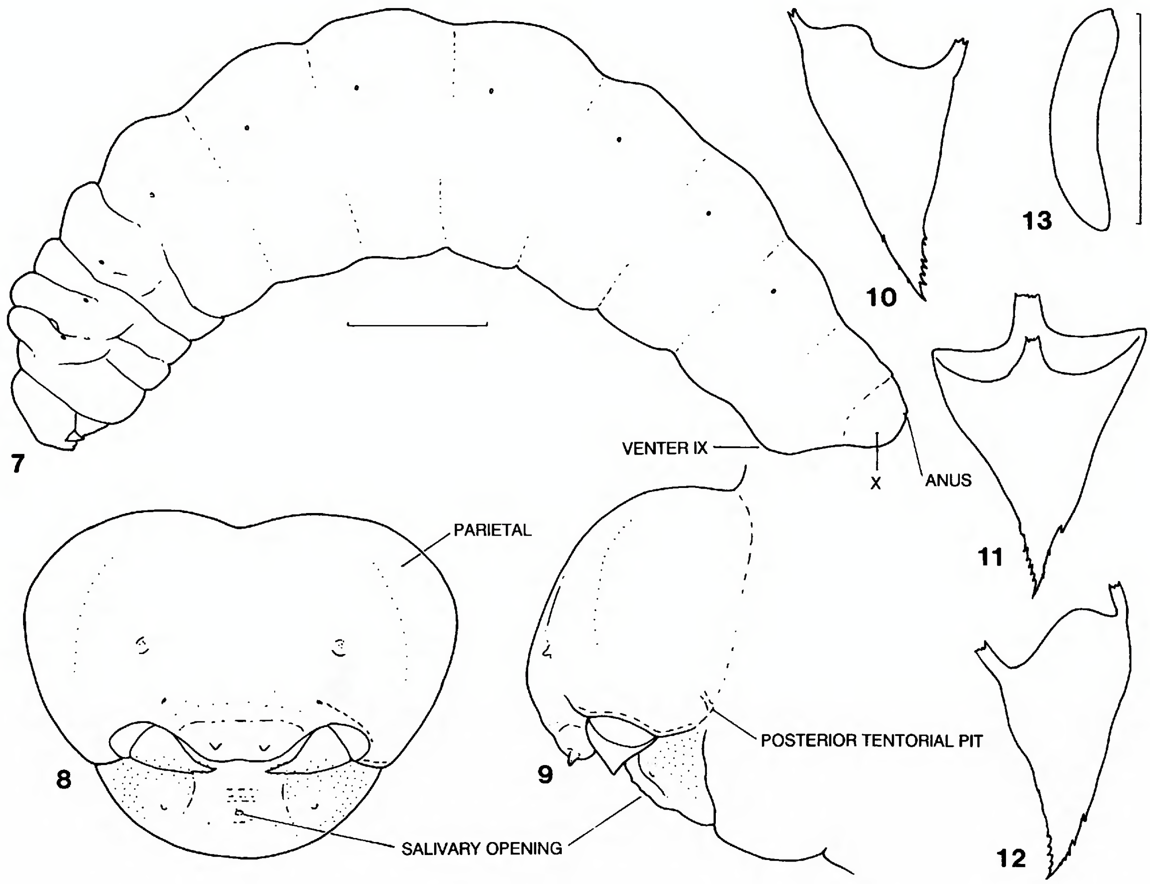
DIAGNOSIS: Like mature or nearly mature larvae of most other Nomadinae, this larva possesses small but distinct paired labral tubercles, recessed labiomaxillary region (indicating absence of cocoon spinning), greatly reduced or lost posterior thickening of the head capsule, posterior tentorial pits that are not structurally tied into the posterior thickening or to the hypostomal ridge, mandibles that are so short that their apices do not meet when closed, and labial palpi that are so reduced that each is represented only by a single sensillum.

Neopasites cressoni, Neolarra pruinosa, and *Townsendiella pulchra,* as mature or nearly mature larvae, are the only Nomadinae which have a frontoclypeal area that is enlarged and overhangs a reduced labrum and which have a protruding venter to abdominal segment X. *Townsendiella pulchra* can apparently be distinguished from the other two taxa because it alone has its parietals so enlarged that the head capsule appears to have a median depression when viewed from the front (fig. 8).

TOTAL LENGTH: Approximately 4.0 mm.

HEAD (figs. 8, 9): Integument of head capsule with scattered, minute, nonsetiform sensilla; maxilla spiculate, especially strongly so on side; epipharynx and hypopharynx nonspiculate. Integument unpigmented except for anterior part of hypostomal ridge and mandibular bases.

Head size normal in relation to rest of body; head capsule much wider than length measured from top of vertex to level of lower margin of clypeus as seen in frontal view. Tentorium thin but complete except apparently for anterior arms; anterior tentorial pits small, low on face; posterior tentorial pit small, in line with hypostomal ridge and apparently lying in unpigmented thin posterior extension of ridge; posterior pit near posterior margin of head but posterior margin of head without ridge and therefore difficult to define; hypostomal ridge moderately developed anteriorly but almost disappearing near posterior tentorial pit; ridge without dorsal



Figs. 7–13. *Townsendiella pulchra.* **7.** Last-stage larva, lateral view. **8, 9.** Head of same, frontal and lateral views. **10–12.** Right mandible of same, dorsal, inner, and ventral views; sensilla and spicules not shown. **13.** Mature oocyte, side view, anterior end at top. Scale lines (both = 1 mm) refer to figures 7 and 13, respectively.

ramus; pleurostomal ridge weakly developed; epistomal ridge weakly developed laterad of anterior tentorial pits, absent between pits; external epistomal depression not evident. Parietal bands faint but evident. Antennal prominences not developed; antennal disc moderate in size; antennal papilla small but pronounced, nearly as long as basal diameter; each papilla bearing three sensilla. Vertex rounded as seen from side and evenly grading into frontal area; parietals enlarged so that, when head viewed from front (fig. 8), parietals bulge on either side of midline; clypeus normal in length; frontoclypeal area in lateral view (fig. 9) bulging beyond base of labrum as is characteristic of last instars of *Neopasites* and *Neolarra* (Rozen, 1966). Labrum small, recessed; labral sclerite not evident; small but distinct, paired labral tubercles arising from labral disc; labrum perhaps faintly emarginate apically; epipharynx not produced ventrally.

Mandibles (figs. 10–12) short so as not to meet apically, stout at base, tapering gradually to apices, and with outer surface spiculate; mandible normally curved, not nearly as straight as in *Neopasites*; adoral surface perhaps somewhat short compared with outer surface, but not nearly as short as described for *Neopasites* (Rozen, 1966); adoral surface at base not produced; mandibular apex bearing sharp teeth on both dorsal and ventral edges; apex appearing rotated so that dorsal dentate edge adoral (as also apparently true in *Neopasites*). Labiomaxillary region recessed and fused although apex of maxillae distinct from labium; maxillary sclerites not discernible; maxillary palpus small, shorter

than basal diameter, and less pronounced than antennal papilla; galea absent. Labium not divided into prementum and postmentum; premental sclerite not defined; labial palpus not produced, represented by single sensillum. Salivary opening a small hole, without lips; hypopharynx not projecting as distinct lobe, but hypopharngeal region extending forward above salivary opening as seen in lateral view, about as in *Neopasites cressoni* (Rozen, 1966: fig. 74); boundary between labium and hypopharynx poorly defined.

BODY: Integument without setae but many areas finely, distinctly spiculate; abdominal segment X not spiculate ventrally. Body without spines or sclerotized tubercles. Body form slender (as might be expected in larva that was not fully fed); intrasegmental lines not evident; body segments without dorsolateral tubercles or other tubercles or swellings except venter of abdominal segment IX distinctly produced, similar to same regions of *Neopasites cressoni* and presumably *Neolarra pruinosa* (Rozen, 1966: figs. 72, 79); abdominal segment X small, without dorsal ridges, and seemingly positioned somewhat dorsally on IX; anus apparently dorsal. Spiracles small, subequal in size, appearing similar to those of *Neopasites cressoni* (Rozen, 1966: fig. 73) although with fewer subatrial chambers. Sexual characters unknown.

MATERIAL STUDIED: One late-stage larva, 8 mi northwest Wickenburg, Maricopa Co., Arizona, May 8, 1990 (J. G. Rozen) from nest of *Hesperapis larreae.*

REMARKS: Comparison of this larva with larvae of other Nomadinae is hampered because it is not mature and not even certainly a last instar. For that reason and because a phylogenetic reevaluation of the mature larvae of the entire subfamily needs to be undertaken, we will not attempt a larva-based detailed assessment of relationships of *Townsendiella* with other Nomadinae here. The close similarity between *Townsendiella* and *Neopasites* (Biastini) is reflected in the above description and many of these characters are probably synapomorphies. Similarities with larval *Neolarra* are also evident although not so pronounced. Whether these similarities are synapomorphies or the result of convergence requires further study, particularly of *Neolarra.*

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